

Review

Effects of Harmful Blooms of Large-Sized and Colonial Cyanobacteria on Aquatic Food Webs

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Abstract: Cyanobacterial blooms are the most important and best studied type of harmful algal blooms in fresh waters and brackish coastal seas. We here review how and to which extent they resist grazing by zooplankton, how zooplankton responds to cyanobacterial blooms and how these effects are further transmitted to fish. Size, toxicity and poor nutritional value are widespread mechanisms of grazing defense by cyanobacteria. In some cases, defenses are inducible, in some they are obligate. However, to some extent zooplankton overcome grazing resistance, partly after evolutionary adaptation. Cyanotoxins are also harmful to fish and may cause fish kills. However, some fish species feed on Cyanobacteria, are able to reduce their abundance, and grow on a cyanobacterial diet. While reduced edibility for crustacean zooplankton tends to elongate the food chain from primary producers to fish, direct feeding by fish tends to shorten it. The few available comparative studies relating fish yield to nutrients or phytoplankton provide no indication that cyanobacteria should reduce the ratio fish production: primary production.

Keywords: cyanobacteria; harmful algal blooms; food web; grazing; zooplankton; fish; eutrophication

1. Introduction

Blooms of large colonial or filamentous Cyanobacteria are the most important and best studied type of harmful algal blooms (HABs) of freshwaters and brackish coastal seas. They play a prominent role in taxonomy-based indices for the assessment of water quality (for a review see Moustaka-Gouni et al. [1]). The relationship of cyanobacterial HABs is double-faced, by being a symptom of water quality deterioration and by further deteriorating water quality [2]. These deteriorating effects include the production of bad odors and toxicity for humans and livestock, oxygen depletion by decaying accumulations of biomass and by alterations of the pelagic food web because of their poor edibility for zooplankton [1]. In this article, we will focus on the food web impacts of cyanobacterial blooms. We will concentrate on the large colonial or filamentous taxa, which usually form HABs, such as the genera *Anabaenopsis*, *Aphanizomenon*, *Dolichospermum* (formerly *Anabaena*), *Microcystis*, *Nodularia*, and *Planktothrix*. We will not deal with picoplanktonic Cyanobacteria, because they occupy a very different position in the pelagic food web.

In the first section, we examine the literature about edibility for zooplankton and the extent to which colony size, toxicity, and poor nutritional value protect cyanobacteria from grazing by zooplankton and how these mechanisms impact the growth and survivorship of zooplankton. This includes also aspects of cyanobacteria–zooplankton co-evolution. In a further step, we examine how these effects translate into community level changes in zooplankton, in particular size structure.

In the second section, we examine the interactions between Cyanobacteria and fish, beginning with the impact of cyanotoxins on fish with a focus on fish kills ascribed to Cyanobacteria, while the

physiological action of cyanotoxins is beyond the scope of our article. We further investigate to which extent Cyanobacteria can be suppressed by the trophic cascade fish–zooplankton–phytoplankton. We further examine the sparse literature about direct fish feeding on cyanobacteria, including the question of a potential top-down control of Cyanobacteria by fish and the possibility of fish to grow on a cyanobacterial diet.

In the third section we examine how the weakening of the phytoplankton–zooplankton–fish trophic chain on one side, and direct feeding by fish on the other side, change the structure of the pelagic food web. In order to test the net effect of these two counteracting mechanisms, we review large-scale comparative studies on the response of biomass and production of various trophic levels to eutrophication.

2. The Cyanobacteria–Zooplankton Interface

2.1. Cyanobacterial Anti-Grazing Strategies

HAB-forming cyanobacteria are generally considered to be inedible or at least poor food for zooplankton [3], mainly because of three common properties: size, toxicity and poor nutritional quality.

2.1.1. Size

Most cyanobacteria have nano-plankton (<20 μm)-sized individual cells, while colony or filament sizes are bigger, reaching the mm- and sometimes even cm-range [4–6]. These large sizes are either reached by gelatinous colonies containing large numbers of individual, coccoid cells (e.g., *Microcystis*) or by forming filaments (e.g., *Anabaenopsis*, *Aphanizomenon*, *Dolichospermum* = *Anabaena*, *Nodularia*, *Planktothrix*) (Figure 1). Some filamentous cyanobacteria achieve a large size not only in length, but also in width by the aggregation of filaments into bundles (e.g., *Aphanizomenon flos aquae*) or by helicoid (e.g., *Dolichospermum spirale*) or curled filaments (e.g., *Dolichospermum flos-aquae*). Within some species (e.g., *Nodularia spumigena*), straight, helicoid, and curled filaments can be found.

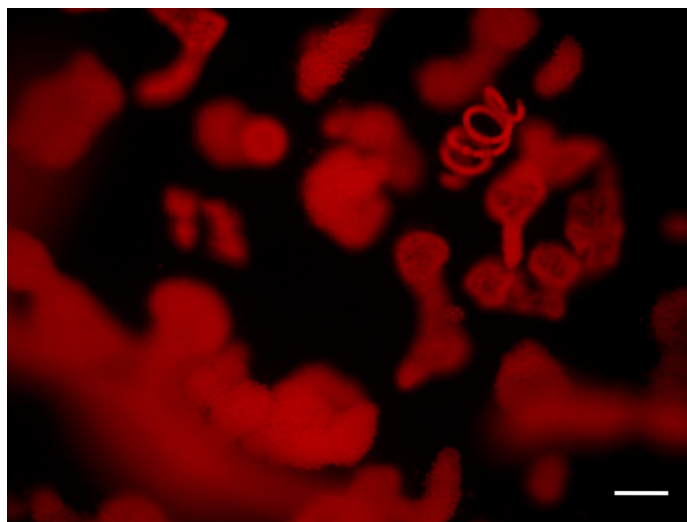


Figure 1. Micrograph of *Microcystis* and *Dolichospermum* forming a cyanobacterial bloom in Lake Kastoria, Greece, epifluorescence microscopy (green excitation). Scale bar: 50 μm .

Most of the early research on the size limits of grazing has been performed with filter-feeding cladocerans, mostly with *Daphnia* [7,8]. Upper size limits are defined by the opening width of mandibles and range from ca. 20 to 50 μm depending on species and age. Exceeding the limit in one dimension offers a relative protection from feeding, exceeding it in two dimensions offers absolute protection.

The issue is more complicated for herbivorous or omnivorous copepods because they can bite off pieces from food particles too large for wholesale ingestion. However, phytoplankton bigger than

several 100 μm are also safe from copepod grazing [9]. Accordingly, Sommer et al. [10] and Woodland et al. [11] found no indication of grazing on wild populations of *Nodularia* dominated by very long filaments, while *Eurytemora*, but not *Acartia* fed on short filaments (mostly $<200\ \mu\text{m}$) of cultured *Nodularia* [12]. In the experiments of Motwani et al. [13], both copepod genera, several Cladocera and rotifers fed on *Nodularia*, but at much lower rates compared to nanoplankton algae.

Protistan grazers select usually smaller food particles than crustacean zooplankton [9], but there are specialists feeding on food items larger than themselves, e.g., the ciliate *Nassula* feeding on filamentous cyanobacteria [14].

2.1.2. Chemical Defense

The widespread toxicity of bloom-forming cyanobacteria has been suggested to have evolved as a defense mechanism against grazing [15]. However, at least the synthesis of microcystin appeared much earlier in phylogeny than metazoans [16], suggesting that the original evolutionary driving force must have been a different from metazoan grazing. Nevertheless, an earlier evolutionary origin does not exclude an anti-grazing effect today, either by deterring grazing or by reducing fitness of grazers.

Active selection between toxic and non-toxic phytoplankton is possible for copepods, which pick individuals, but not for filter feeders like cladocerans [17]. Selective avoidance of various cyanobacteria compared to a green alga based on chemical properties was shown for the freshwater copepod *Diaptomus* [18]. When offered toxic and non-toxic strains of *Nodularia* the brackish water copepod *Eurytemora* fed on both, but with a five times lower grazing rate on the toxic strain [12]. For *Daphnia*, a reduction in the general filtration rate, i.e., also the filtration rates on well edible phytoplankton, by dissolved, extracellular microcystin was shown by Haney et al. [19], while other studies failed to show a response of filtration rates to different concentration of microcystin [20,21]. Zooplankton have been shown to bioaccumulate cyanotoxins, i.e., to have higher concentrations of cyanotoxins in their biomass than in phytoplankton biomass [22].

In addition to toxicity of part of the strains in most bloom-forming species, all cyanobacteria share a low nutritional quality for zooplankton, as documented by slower growth, lower egg production and higher mortality of cyanobacteria-fed animals compared to animals fed by diatoms, most flagellate taxa and heterotrophic protists [23]. The poor nutritional quality is ascribed to a lack of essential fatty acids, in particular polyunsaturated ones [24] and to a lack of sterols [25].

2.1.3. Induction of Defenses

Most defenses against grazing do not come without costs. In the case of size, the main costs of cyanobacteria are lower uptake rates for nutrients and growth rates [9], while the frequently mentioned disadvantage of higher sinking losses does not apply to cyanobacteria because of their ability to float with the help of gas vacuoles. Production of toxins costs the substance and energy invested in the toxins and the enzymes needed for production. Thus, it could be expected that natural selection would favor defense traits which can be switched on and off upon demand, i.e., inducible defenses over constitutive ones [26].

The impression of defense induction is strengthened by the well-known phenomenon that in pure cultures cyanobacteria are often unicellular or short filaments, while in situ large colonies and filaments prevail. However, caution is needed when induction is deduced from the co-occurrence of zooplankton and the prevalence of inedible morphs. It might as well result from selective removal of the edible ones. The same caveat applies to experiments where cyanobacteria are directly exposed to grazers. A conclusive experiment has to include indirect exposure, e.g., growing cyanobacteria in filtrates of zooplankton cultures. An ideal experimental design would also distinguish between chemical signals released by zooplankton themselves and by signals resulting from injured cyanobacteria.

To date, evidence for inducible defenses of cyanobacteria has been rather meager and contradictory. Lynch [27] found that *Aphanizomenon flos-aquae* flakes tend to disintegrate when exposure to *Daphnia* is terminated. Weijnerowski et al. [28] found the induction of filament thickening of *Aphanizomenon gracile*

and *Raphidiopsis raciborskii*, but not of *Planktothrix agardhii* by exudates of *Daphnia* and by sodium octyl sulphate, a commercially available *Daphnia*-kairomone. In a study by Van Gremberghe et al. [29] chemicals derived from *Daphnia* grazing induced colony formation in only 1 out of 8 strains of *Microcystis*. In another study, grazing by the mixotrophic protist *Ochromonas* induced colony formation in *Microcystis*, while metazoan grazers did not [30]. Interestingly, *Ochromonas* was resistant to toxins, while the metazoans were not. Lundgren et al. [31] did not find induction of size increase of *Nodularia* by copepods grazing [31].

Evidence for induction of toxicity is similarly mixed. Jang et al. [32] showed an increase in the microcystin production of *Microcystis aeruginosa* both by direct and indirect exposure (zooplankton filtrate) to several cladocerans (*Daphnia magna*, *D. pulex*, *Moina crocopa*). Conversely, Gorkhova and Engström-Öst [33] and Engström-Öst et al. [34] did not find evidence of toxicity induction by copepods. On the contrary, toxicity even decreased under copepod grazing, which they attributed to release from nitrogen limitation by zooplankton excretion. However, Engström-Öst et al. [34] found that nodularin production was enhanced by the presence of competing algae (the prasinophyte *Tetraselmis suecica* and the cryptophyte *Rhodomonas salina*) and the nodularin had an allelopathic effect on *Rhodomonas*. Sadler and Von Elert [35,36] studied chemical interactions between *Daphnia* and *Microcystis* with a more detailed analysis of secondary metabolites and suggest that hitherto unknown toxins might be induced by grazing. The concentration of most research efforts on microcystin in foregoing research might have led to an underestimation of the importance of defense induction. However, a transcriptomic analysis of the effects of *Daphnia magna* and *pulex* grazing on *Microcystis aeruginosa* showed an upregulation of growth and of heat shock proteins (a general stress response), an increasing abundances of transcripts encoding mucilage production and gas vesicles potentially related to grazer avoidance. However, there was no upregulation of toxin production [37].

2.2. Cyanobacterial Anti-Grazing Strategies

2.2.1. Grazing Inhibition

The dominance of unpalatable, nutritionally poor and sometimes toxic cyanobacteria also affects the utilization of nutritionally better and well edible phytoplankton. It can inhibit feeding on the undergrowth of well edible phytoplankton, in particular the feeding of filter feeding cladocerans. Bigger species are more vulnerable to feeding inhibition than smaller ones [8,38]. Metazoan microzooplankton and heterotrophic protist appear to be much less sensitive to feeding inhibition than cladocerans [39,40]. Sellner et al. [41] reported feeding inhibition of Baltic Sea copepods by *Nodularia*, while Engström et al. [12] did not find an inhibiting effect on *Eurytemora*. Feeding can not only be suppressed by mechanical interference, but also by also toxins, for example by dissolved microcystin [19] or by toxins from ingested filament fragments of *Anabaena* [42].

2.2.2. Vital Rates of Zooplankton

Because of their poor palatability, feeding inhibition, low nutritional value, and potential toxicity, it is no surprise that cyanobacteria have the potential to reduce somatic growth rates and reproductive rates of zooplankton while increasing mortality.

Different *Daphnia* species grow more slowly when exposed to increasing concentrations of *Aphanizomenon*, but smaller species are less sensitive [43]. Thresholds of palatable food needed for minimal somatic growth are generally smaller for larger cladoceran species, but become larger when cyanobacteria are added [44,45]. Negative effects of the ingestion of *Nodularia* on the growth of the copepod *Acartia* were shown by Motwani et al. [13].

DeMott et al. [46] tested the sensitivity of three *Daphnia* species and one copepod (*Diaptomus*) to purified microcystin-LR and nodularin as well as to live *Microcystis* and found increased mortality in all cases, although with different sensitivities depending on zooplankton species and nature of the toxin. Similarly, Rohrlack et al. [20] found a reduced survival time of several clones of *Daphnia* in response to

the ingestion of toxic *Microcystis* cells. In a further study, the physiological effect of microcystin on *Daphnia* was evaluated in detail [47]. Using microcystin-LR treated food (freeze dried *Chlorella* cells) Wilson and Hay [48] showed that one clone of *Daphnia pulicaria* was harmed by microcystin, while the other was not.

Gilbert [42] showed an increase in *Daphnia* mortality following the ingestion of *Dolichospermum* (called *Anabaena*) while rotifers were unaffected, because they could not ingest *Dolichospermum*. Feeding on *Nodularia* increased the mortality of *Acartia* in a study by Lundgren et al. [31] while it was not harmed by *Nodularia* in the study of Engström et al. [12], where it avoided feeding on *Nodularia*. Aqueous extracts from two different cyanobacterial blooms in the Curonian Lagoon (Lithuania/Russia) lead to increased *Daphnia*-mortality in one case, but not in the other [49].

2.2.3. Zooplankton Defense

Obviously the most straightforward defense strategy of zooplankton against cyanobacteria would be avoidance. As demonstrated by several of the examples mentioned above [12,17,18,42] copepods and rotifers can avoid ingestion by selective feeding, while non-selective filter feeders like cladocerans can only reduce overall filtration rates. This can only be a feasible strategy when phytoplankton is distributed in a patchy manner [50], otherwise the filter feeders would have to pay by ingesting less food. The widespread lower sensitivity of smaller zooplankton is also due to the lower size limit of their food ingestion, if cyanobacterial biomass is dominated by large colonies and filaments and accompanied by an “undergrowth” of small fragments or single cells.

As shown by the examples provided above, physiological tolerance of toxins is highly specific both in terms of the toxin and the zooplankton species, or even strain. However, there seems a general trend that ciliates are less sensitive to microcystin than crustacean zooplankton. Copepods are far more sensitive than the cladocerans, with order of magnitude differences between the groups [51]. However, some degree of tolerance by detoxification can be acquired when zooplankton are exposed to toxic cyanobacteria. Tolerance to cyanotoxins can be achieved by induction during the lifetime of an individual [52], by maternal transmission to offspring [53] or by evolutionary selection for tolerance [54]. However, the induction of resistance and induction of toxicity might be a mutual arms race. Akbar et al. [55] found that *Daphnia*, which had acquired some tolerance by maternal transmission, had a reduced fecundity and survival when fed with *Microcystis* previously exposed to resistant *Daphnia* compared to feeding with unexposed *Microcystis*. A comparison of *Daphnia* germinated from differently aged resting eggs of the sediment of Lake Constance showed an increasing resistance to cyanotoxins during the period of eutrophication and a return to less resistant genotypes during recovery from eutrophication at decadal time-scales [54,56]. The decline in resistance during recovery from eutrophication indicates that resistance must involve fitness costs, although there are only few studies examining those costs [57,58]. Chislock et al. [59] found that *Daphnia* with a long evolutionary history of co-occurrence with toxic *Raphidiopsis* could control a *Raphidiopsis* bloom in mesocosms, while *Daphnia* previously unexposed to *Raphidiopsis* could not. Note that the grazing defense was mainly toxicity, while the morphological defense was only imperfect, because *Raphidiopsis* can exceed 50 µm in only one dimension.

2.2.4. Shifts towards Smaller Zooplankton Species

It is obvious from the examples above, that smaller zooplankton usually experience smaller fitness losses from blooms of cyanobacteria than larger ones. Therefore, it is a straightforward expectation that a shift towards smaller zooplankton should also be observed in situ, as has already been reported by Gliwicz [8], during a seasonal analysis in a eutrophic lake in Poland. Meanwhile, this observation has been confirmed frequently. To mention just a few examples: the shifts towards smaller zooplankton under cyanobacterial dominance have also been found in an inter-lake comparison of mainly cold-temperate and boreal lakes [60]. DeMott et al. [61] reported the exclusion of large-bodied *Daphnia* species in hypertrophic Dutch lakes. Hansson et al. [62] reported the shift towards smaller

zooplankton driven by cyanobacteria from Scandinavian lakes. In the hypertrophic Greek lakes Voulkaria and Pamvotis, a dominance of the small-sized cladoceran genera *Bosmina* and *Chydorus* coincides with cyanobacterial blooms [63]. Similarly, Moustaka-Gouni et al. [64] reported an overall small size (up to 0.3 mm) of zooplankton in the Greek Lake Kastoria with a history of toxic cyanobacterial blooms. In this lake, a double effect of a succession of toxic blooms (*Cylindrospermopsis*, *Aphanizomenon* and *Microcystis* species) on the microbial food web structure was also observed. Leonard and Paerl [65] found a shift towards smaller zooplankton during a bloom of *Raphidiopsis* in a subtropical system in Florida. As a consequence of the suppression of large zooplankton, Christoffersen et al. [66] found increasing importance of the carbon- and energy flux through the microbial loop, with special importance of ciliates, during an *Aphanizomenon* bloom in a Danish lake.

However, some caution is needed when interpreting field data, because the same shifts in zooplankton size structure can also result from fish predation [67,68], because zooplankton-feeding fish are visual predators preferring large zooplankton as prey. In particular, they prefer large *Daphnia* species, because they cannot escape as quickly as large copepods.

3. The Cyanobacteria–Fish Interface

3.1. Fish Kills

Cyanotoxins are also harmful to fish, either by oral ingestion of cyanobacteria or as solutes in water, often released during the decay of blooms [69–71]. Cyanotoxin concentrations in fish biomass indicate biodilution instead of biomagnification, as has been found for zooplankton [22]. While fish, in particular cyprinids, often coexist with cyanobacteria showing little or at least only sub-lethal effects, often cyanobacterial blooms are associated with mass mortality of fish (“fish kills”).

Fish kills associated with cyanobacterial blooms occurred during or after blooming of various bloom-forming cyanobacteria taxa and affected a variety of fish taxa [72]. Sometimes the authors mention a single victim taxon, but it is not always clear whether this is the only important fish species in the particular lake or the only one affected severely among several fish taxa. Examples include brown trout mass mortality in Loch Leven associated with a *Dolichospermum*-bloom in Loch Leven, Scotland [73], a stickleback mass mortality associated with a *Nodularia* bloom in the Gulf of Finland, Baltic Sea [74], catfish mass mortality associated with *Microcystis* in fish ponds [75], and a massive mortality of tilapias associated with blooms of *Raphidiopsis* and *Microcystis* in Lago Paranoa, Brazil [76]. Fish kills affecting several species in a water body were associated with *Aphanizomenon*-bloom in Sempacher See, Switzerland [77] and Lake Vistonis, Greece [78] and blooms of several cyanobacteria (*Aphanizomenon*, *Dolichospermum*, *Microcystis*) in Lake Peipsi, Estonia–Russia [79].

Sometimes, the assignment of cause and effect relationships might be difficult, even if fish kills coincide temporally with cyanobacterial blooms because of a temporal coincidence with other potentially lethal factors, such as oxygen depletion or blooms of other toxic algae. In brackish inland waters, estuaries, coastal lagoons and other transitional waters cyanobacteria blooms may coexist with other toxic algae, such as the flagellate *Prymnesium parvum*. Lindholm et al. [80] report a fish kill from brackish Lake Vargsundet, Finland, where mass developments of the toxic cyanobacterium *Planktothrix agardhii* and *Prymnesium* were separated vertically. Fish died in the *Prymnesium*-dominated epilimnion, while they survived in the *Planktothrix*-dominated metalimnion. In the brackish water Lake Karla, Greece, two consecutive fish kills coincided with a cocktail of potentially toxic cyanobacteria and algae, dominated by *Planktothrix* cf. *agardhii*, *Prymnesium parvum*, and *Pfiesteria* cf. *piscicida* [81] while a recent fish kill in 2018 coincided with a monospecific bloom of *Prymnesium parvum* (Moustaka-Gouni et al. unpublished data). In another Greek brackish waterbody, Lake Koronia, a conspicuous fish kill in 2019 coincided with a mixture of potentially toxic cyanobacteria (*Anabaenopsis*, *Arthrospira*) and *Prymnesium parvum* (Moustaka-Gouni et al., unpublished data). In this lake, cyanobacterial and *Prymnesium* blooms coincided with fish and bird kills in 2004 [82]. Episodes of the fish-eating pelican (*Pelecanus crispus*) mortality coincided with toxic cyanobacteria blooms in Lake Karla [83]. McInnes and

Quigg [84] hypothesize that the recurrent mass mortality of menhaden in coastal embayment in Texas, USA might be a joint effect of cyanobacterial toxins and hypoxia caused by the degradation of cyanobacterial biomass.

3.2. Cascade Effects of Fish on Phytoplankton

Simultaneous with the development of the trophic cascade theory [85], applied limnologists suggested using biomanipulation by fish removal [86] as tool to improve the water quality of eutrophicated lakes for cases where nutrient abatement was not considered feasible or too slow. The idea is the following: if zooplankton-feeding fish are removed or strongly reduced, a release from predation pressure should lead to a dominance of large-bodied zooplankton, in particular *Daphnia*, which are more efficient in controlling phytoplankton biomass development, leading to an increase in water clarity. The idea is in perfect agreement with cascade theory, but appears to contradict the existing knowledge that large colonies of harmful cyanobacteria are inedible or poorly edible even for larger *Daphnia* spp. (upper size limit for food particles ca. 50 µm in at least two dimensions). In reality, biomanipulation has been successful in some cases, but not successful in other cases. In Shapiro's pilot experiment in Round Lake, zooplankton mean body length increased from ca. 0.3 mm before fish removal to 0.8–1.1 mm in the year after fish removal by the toxin rotenone and chlorophyll concentrations decreased compared to the year before. However, in the following year zooplankton size stayed high, but in summer a bloom of bundle-forming *Aphanizomenon* developed [86]. In eutrophic lake Ringsjön (Sweden) the success of biomanipulation by fish removal was mediated by the joint action of selectively feeding copepods and non-selective *Daphnia* [87,88]. In contrast, cyanobacterial blooms were favored by copepod grazing in North American Lake Vancouver [89,90].

Overall, there have been successful and unsuccessful cases of biomanipulation. In a meta-analysis of 54 studies, Brett and Goldman [91] found strong effects on phytoplankton in ca. 1/3 of the reviewed cases and weak ones in the remaining studies. When phytoplankton escapes from top down control by zooplankton in spite of fish removal, cyanobacteria are the usual drivers of this escape [92,93]. Meanwhile, the spectrum of biomanipulation methods has been broadened and includes stocking with piscivorous fish, stocking with filter-feeding fish and stocking with filter-feeding bivalves. Triest et al. [94] found a success rate of ca. 2/3 in an overview of 34 studies.

Benndorf et al. [95] considers phosphorus export from the epilimnion and subsequent phosphorus impoverishment of the epilimnion during summer as key mechanism to prevent cyanobacteria blooms during summer. Large zooplankton, like *Daphnia*, serve as promoters of P-export because by feces production and vertical migration. If P-loading is too strong, the export effect would not be strong enough. Benndorf et al. [95] suggest a biomanipulation efficiency threshold of total P-loading of 0.6 to 0.8 g TP m⁻² year⁻¹, above which biomanipulation becomes inefficient. Their line of reasoning is tailored to stratifying lakes in the boreal and cold-temperate zone. In this zone, a spring bloom of edible phytoplankton is followed by a grazing-induced clear water phase and large poorly edible algae only can come up after the clear water phase [60,96]. In shallow lakes, improvement in the light climate and binding of phosphorus by expanding macrophytes might replace the role of sedimentary P-losses [97]. In warmer climate lakes without clear water phase [98], biomanipulation by fish removal might be no option at all, because of the too large overwintering populations of cyanobacteria. Grazing is less efficient in removing blooms than in preventing the onset of blooms. Gliwicz [99] found that fish removal can only be effective when *Daphnia* grazing intervenes before a critical density of cyanobacteria is exceeded (1–10 µg C L⁻¹) if large-bodied *Daphnia* species should be promoted.

Daphnia also influences nutrient cycles by its impact on N:P ratios [100]. As an animal with a high P-content in biomass, *Daphnia* tends to assimilate N and P at relatively low ratios and, consequently, excretes N and P at high ratios, thus reducing the competitive advantage for N₂-fixing Cyanobacteria.

The question of timing is also relevant for the possibility of grazers to overcome the morphological defense of cyanobacteria. Before colonies exceed the size limit of edibility, they have to grow up from single cells, akinetes or fragments. Thus, they have to pass through a window of vulnerability

during which efficient grazers can prevent the development of a bloom. As argued by Sommer [101], the cyanobacteria-dominated state and the grazer-dominated state might be viewed as alternative stable states which sometimes depend on tiny differences in the initial conditions, making the effectivity of biomanipulation sometimes unpredictable (Figure 2).

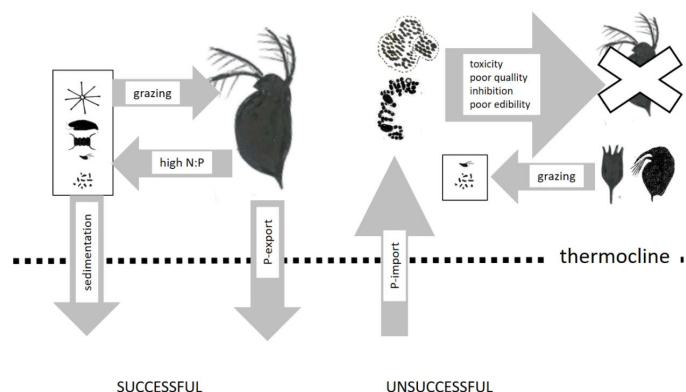


Figure 2. Idealized mechanisms stabilizing the successful and the unsuccessful state of biomanipulation by removal of planktivorous fish.

The Cyanobacteria-dominated state is enforced by the ability to sequester metalimnetic nutrients by vertical migration [102] and by the multitude of negative effects on large zooplankton discussed above. In addition, the failure of grazer control reduces nutrient recycling and permits the built-up of a strongly nutrient limited biomass, which, even in the case of edibility would not satisfy the P-demand of zooplankton, in particular *Daphnia* [103]. The grazer-dominated, clear water state is stabilized by the zooplankton-driven export of particulate P, recycling of dissolved P by zooplankton and, therefore, the persistence of a high P-content and therefore high nutritional quality of the phytoplankton.

Thus, trophic cascade effects from fish to primary producers affect Cyanobacteria only in part of the cases. Stronger effects are expected in more seasonal climates and under only moderate eutrophication, but there remains a strong degree of unpredictability.

3.3. Fish Feeding on Cyanobacteria

Cyanobacteria were found at the gill rakers and in the gut contents of filter-feeding fish decades ago. However, this was often seen as a kind of accidental ingestion because cyanobacterial colonies overlap in size with the targeted mesozooplankton food [104]. It was even shown that gelatinous cyanobacteria like *Microcystis* benefitted from ingestion because of fertilization during live gut passage [105,106]. However, several studies in tropical and subtropical regions have shown that filter feeding fish can decimate cyanobacterial blooms [106–110] and, therefore, substitute for a failure of top-down control by zooplankton. In an enclosure experiment, Radke and Kahl [111] found that silver carp was able to control cyanobacteria, but not smaller phytoplankton because it reduced *Daphnia* at the same time. Control of cyanobacteria was reported to date from silver carp (*Hypophthalmichthys molitrix*), a fish of East Asian origin, and from subtropical/tropical tilapia (*Oreochromis* spp.). The typical benthic-pelagic fish of eutrophic lakes in colder regions, like bream (*Abramis brama*) and roach (*Rutilus rutilus*), have not been reported to suppress Cyanobacteria, in spite of the ingestion of Cyanobacteria. On the contrary, invasion by bream-enhanced cyanobacterial dominance in a North Italian lake [112], most probably by stirring up the sediment and enhancing P-release from the sediment [113]. However, silver carp is expanding in Europe and North America because of stocking, often motivated by its ability to reduce Cyanobacteria.

To date, there are only few studies demonstrating the successful growth of fish on a predominantly cyanobacterial diet. Kamjunke et al. [114] found that roach lost body weight when fed with *Microcystis* or, not being fed, stayed more or less equal when fed with *Aphanizomenon* and grew when fed with *Daphnia*.

The efficient usage of a cyanobacterial for fish growth was shown by the analysis of fatty acids and stable isotopes in fish biomass during a cyanobacterial bloom in the coastal Lake Hachiro, Japan [115]. The fish species growing on cyanobacteria belonged to the families Cyprinidae (common carp: *Cyprinus carpio*, crucian carp: *Carassius* sp.), Gobiidae (*Tridentiger brevispinis*, *Gymnogobius castaneus*), and Osmeridae (*Hypomesus nipponensis*). *Cyprinus* and *Carassius* are widely distributed, while the other three species are East Asian in distribution. There is definitely demand for further research, in particular with respect to the benthic-pelagic fish typical of eutrophicated lakes in the temperate and boreal zones.

4. Food Web Structure and Production of Animal Trophic Levels

4.1. Food Web Structure

The reduced edibility of cyanobacteria for mesozooplankton and the ability of some fish species to feed on cyanobacteria can lead to two different types of restructuring the pelagic food web when cyanobacteria replace small- and medium-sized phytoplankton (Figure 3).

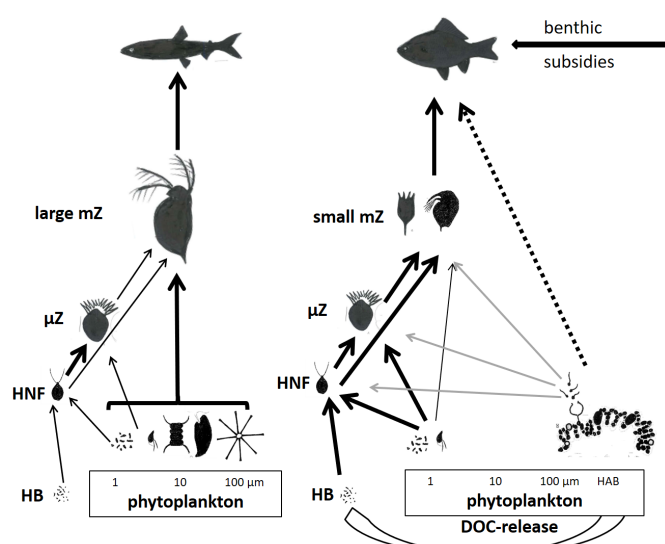


Figure 3. Major trophic pathways to plankton-feeding fish under two scenarios of the pelagic food web, left: oligotrophic scenario with *Daphnia* as main mesozooplankton and coregonids as main planktivore fish, right: eutrophic scenario with Cyanobacteria as main phytoplankton and cyprinid fish as main planktivores. Thick arrows: feeding pathways more important than in the other scenario; thin arrows: feeding pathways less important than in the other scenario; dotted arrow: feeding pathway only realized with fish feeding on Cyanobacteria; grey arrows: matter and energy transfer via release of zoospores by fungal parasites; open, bent arrow: matter and energy transfer via DOC (dissolved organic carbon)-release by senescent Cyanobacteria. Abbreviations: HB: heterotrophic bacteria; HAB: harmful algal blooms; HNF: heterotrophic nanoflagellates; μ Z: microzooplankton; mZ: mesozooplankton.

If small- and medium-sized phytoplankton dominate the primary producer trophic level a big portion of primary production is directly consumed by mesozooplankton, in many lakes by *Daphnia*. This pathway of carbon and energy flow is further strengthened by feeding of mesozooplankton on heterotrophic protists and subsequent reduction in their competitors, a kind of “eating your competitor strategy” [116]. Plankton-feeding fish then feed on mesozooplankton, leading to a short food chain with mesozooplankton at trophic level 2 to 3 and planktivorous fish close to trophic level 3 to 4. If fish feeding on cyanobacteria are lacking, most of the cyanobacterial biomass is not consumed directly by zooplankton but decays at the end of blooms, the decay being possibly enhanced by viral lysis. The subsequent release of DOC stimulates bacterial growth and bacterial production becomes a major carbon and energy source of higher trophic levels [117]. The bacteria are preyed upon by heterotrophic nanoflagellates and microzooplankton, which then serve as food for mesozooplankton. There might

also be some transfer of cyanobacterial production to mesozooplankton by chytrid parasitism on Cyanobacteria, release of zoospores and zooplankton feeding on zoospores [118,119]. Due to the detrital and the parasitic loop, mesozooplankton are at trophic level 3 to 4. This food chain elongation is predicted to lead to increased losses of carbon on the energy on the pathway towards fish, and thus to a lowered ratio of fish production to primary production (FP:PP) [120]. However, if fish are able to feed on cyanobacteria, as in the example by Fujibayashi et al. [115], the food chain will not be elongated, but shortened. This leads to the prediction of a higher FP:PP ratio.

4.2. N-Fertilization of Food Webs

Under nitrogen limitation transfer of nitrogen fixed by cyanobacteria to higher trophic levels zooplankton becomes an important issue. While it has traditionally been assumed that fixed nitrogen becomes available only after the decay of blooms, more recent studies using stable isotopes have shown a rather rapid transfer of freshly fixed nitrogen to mesozooplankton [11,121–124]. Thus, either the direct grazing or release of DON, uptake by bacteria and bacterivorous protists must be accounted for in the transfer to mesozooplankton. Wannicke et al. [123] ascribed ca. one to two thirds to direct the grazing of Baltic Sea copepods on cyanobacteria (mainly *Nodularia spumigena* and *Pseudanabaena*), while, in the studies of Sommer et al. [10], Woodland et al. [11] and Loick-Wilde et al. [123], the microbial pathway appeared responsible for most of the transfer from *Nodularia* to mesozooplankton.

4.3. Impacts on an Animal Biomass and Production

Poor edibility for zooplankton, adverse effects on fish and elongation of food chains should negatively affect the production of metazoans in water bodies dominated by cyanobacteria. On the other hand, the direct feeding of fish on cyanobacteria and channeling of additional nitrogen into the ecosystem could have the opposite effect. Surprisingly, the available literature is quite meager. Even in those cases where the primary production and production of animal trophic levels have been measured in cross-system analyses or in long-term analyses of single water bodies, animal production has usually been related to some proxy of trophic state (e.g., total phosphorus, phytoplankton biomass, chlorophyll) but not to the metrics of Cyanobacteria. While there is a general trend that larger colonial or filamentous Cyanobacteria become more abundant with increasing eutrophication [125], it is often not possible to decide whether general eutrophication effects, e.g., hypoxia in deep water or at the sediment surface, or specific effects of Cyanobacteria are responsible for the response of secondary production.

4.3.1. Studies within Restricted Regions

Gerdeaux et al. [126] analyzed the change in fish yields in 11 per-alpine lakes in Switzerland and France during recovery from eutrophication with total phosphorus (TP) ranging from 2–135 $\mu\text{g L}^{-1}$. Fish yields increased with TP only up to a threshold of 20 $\mu\text{g L}^{-1}$ and a plateau above, suggesting a decline of the FP:PP-ratio with eutrophy. Quite typical for central and northern European deep lakes, salmonids and coregonids dominated in the low-nutrient range, percids in the intermediate range and cyprinids in the upper range [127]. Jeppesen et al. [128] compared 71 shallow lakes in Denmark ranging from 20 to 1000 $\mu\text{g TP L}^{-1}$ and found a decreasing zooplankton: phytoplankton ratio along with increasing TP. Catch fish per unit effort of planktivorous fish increased with TP, but far less than linear. Both findings suggest a decreased transfer efficiency at increasing eutrophication. Perch (*Perca fluviatilis*) was the dominant fish at the low end of the TP gradient, while the cyprinids roach and bream profited from eutrophication. While these studies did not specifically look for the effect of cyanobacteria, coregonids as pelagic spawners seem to suffer primarily from their eggs sinking to hypoxic conditions in deep water or at the sediment surface [129], while cyprinids might profit from the ability to feed on cyanobacteria.

4.3.2. Large Scale Surveys

Comparative studies across larger regions relating the biomass or production metrics of different trophic levels to each other or to nutrient richness (usually characterized by TP) were mainly conducted during the time when lake eutrophication came to be appreciated as a major environmental problem and the key role of phosphorus had to be established [130,131]. Fish production in those studies was not directly measured but replaced by the surrogate parameter fish yield, which unfortunately neglects species not targeted by fisheries. Statistical relationships between the different metrics were most commonly expressed by the equation

$$y = a \times x^b \quad (1)$$

If x is an animal-related metric, a decreased efficiency of the energy and matter flow from phytoplankton to animal trophic levels would be expressed by the exponent b of the relationship of an animal metric to TP lower than the corresponding exponent for phytoplankton. Unfortunately, the results of these studies (Table 1) permit no firm conclusion, although an almost linear relationship between TP and the biomass of cyanobacteria was confirmed by Smith [125]. Otherwise, the exponents for the different trophic levels differ considerably between the different studies, e.g., from 0.96 to 1.44 for the different metrics of phytoplankton biomass [130–132]. Part of these discrepancies is certainly due to the different collections of lakes included and, possibly even more importantly, the different seasonal coverage of data from annual to summer means and even annual maximal values. Interestingly, zooplankton biomass values increase clearly less than linearly with TP [133,134], while annual fish yield increases linearly with TP [135] and with primary production [136]. This would be consistent with the assumption that cyanobacteria indeed weaken the phytoplankton–zooplankton–fish pathway in the food web, but that fish compensate via feeding directly on cyanobacteria [115]. However, one has to consider that estimates of fish yield include benthic and benthic-pelagic fish, which rely at least in part on other primary carbon sources than phytoplankton production. This might induce a bias in multi-lakes statistics because benthic subsidies are more important in the biological production of shallower lakes and those lakes are overrepresented in the upper end of the oligo- to eutrophic gradient.

Table 1. Relationships between phytoplankton, zooplankton, fish and nutrient metrics: Taken from published multi-lake comparison according to the regression model $y = a \times x^b$. Values are mean values for the seasonal coverage indicated in the first two columns, except for one case where the annual maximum of chlorophyll was used. The primary production–chlorophyll relationship by in [129] is based on individual measurement and not on lake means.

Dependent Variable	Independent Variable	a	b	Source
Phytoplankton				
Chlorophyll, summer ($\mu\text{g L}^{-1}$)	TP, spring ($\mu\text{g L}^{-1}$)	0.073	1.44	[130]
Chlorophyll, annual ($\mu\text{g L}^{-1}$)	TP, annual ($\mu\text{g L}^{-1}$)	0.28	0.96	[131]
Chlorophyll, annual maximum ($\mu\text{g L}^{-1}$)	TP, annual ($\mu\text{g L}^{-1}$)	0.64	1.05	[131]
Wetweight, growing season ($\mu\text{g L}^{-1}$)	TP, growing season ($\mu\text{g L}^{-1}$)	30	1.4	[132]
Cyanobacteria, wwt, growing season ($\mu\text{g L}^{-1}$)	TP, growing season ($\mu\text{g L}^{-1}$)	43	0.98	[125]
Primary production, annual ($\text{g C m}^{-2} \text{ year}^{-1}$)	TP, annual ($\mu\text{g L}^{-1}$)	31.1	0.54	[131]
Primary production, growing season ($\text{g C m}^{-2} \text{ day}^{-1}$)	Chlorophyll, growing season ($\mu\text{g L}^{-1}$)	30.6	0.927	[136]
Zooplankton				
Dry weight, ice free season ($\mu\text{g L}^{-1}$)	TP, ice free season ($\mu\text{g L}^{-1}$)	38	0.64	[134]
Crustacean dwt, ice free season ($\mu\text{g L}^{-1}$)	TP, ice free season ($\mu\text{g L}^{-1}$)	5.7	0.91	[133]
Crustacean dwt, seasonal coverage not uniform between study lakes ($\mu\text{g L}^{-1}$)	Chlorophyll, ice free season ($\mu\text{g L}^{-1}$)	27.5	0.53	[133]
Fish				
Wet weight (mg m^{-2})	TP, annual ($\mu\text{g L}^{-1}$)	590	0.71	[135]
Yield ($\text{mg wwt m}^{-2} \text{ year}^{-1}$)	TP, annual ($\mu\text{g L}^{-1}$)	7.1	1.02	[135]
Yield ($\text{mg wwt m}^{-2} \text{ year}^{-1}$)	Primary production ($\text{mg wwt m}^{-2} \text{ year}^{-1}$)	0.0023	0.90	[136]

5. Conclusions

- Filamentous and large colonial Cyanobacteria resist zooplankton grazing by size, toxicity and low nutritional values;
- Grazing resistance is not complete. Thus, cyanobacteria are not a complete dead end in the food web;
- There is an evolutionary arms race between cyanobacterial grazing resistance and zooplankton ability, to overcome grazing resistance;
- Cyanobacteria drive zooplankton composition towards species of smaller body size, thus reducing the potential for top-down control on phytoplankton;
- Top-down control of cyanobacterial blooms by large zooplankton is more effective in the preventing the onset of blooms than in controlling already-developed blooms;
- *Daphnia*. can reduce the competitive advantage for cyanobacteria by fecal sedimentation and increase the competitive advantage of nitrogen-fixing cyanobacteria by a reduction in N:P supply rates;
- Fish can be harmed by cyanobacterial toxins, harmful effects sometimes even leading to fish kills;
- However, coexistence of fish, often cyprinids, with cyanobacterial blooms is often observed;
- Cyanobacterial dominance in phytoplankton reduces the efficiency of matter and energy transfer from primary production via zooplankton to fish;
- Chytrid parasites might transfer part of primary production from cyanobacteria to mesozooplankton through zoospores ingested by zooplankton;
- Obligate and facultative filter-feeding fish have been found to ingest cyanobacteria;
- Some fish species (silver carp and tilapia) can exert top-down control on cyanobacteria;
- Some fish species can grow on a cyanobacterial diet;
- Further research is needed, to see whether this applies also to widespread benthic-pelagic fish like bream and roach;
- The probability of fish kills increases with increasing eutrophication and with increasing cyanobacterial and other harmful algal blooms;
- To date, there is no firm evidence that the ratio of fish production: to primary production declines with eutrophication or increased cyanobacterial biomass, as long as there are no fish kills. Multi-lake surveys with simultaneous measurements of primary production, phytoplankton and cyanobacterial biomass, zooplankton and fish production are needed.

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